Ultrastructures of antennal sensilla of adult females of *Porphyrophora sophorae* (Coccoidea: Margarodidae)

WANG Xu[1], XIE Ying-Ping[1,*], ZHANG Yan-Feng[1], LIU Wei-Min[1], WANG Quan-Liang[2]

(1. School of Life Science, Shanxi University, Taiyuan 030006, China;
2. Xiangfen Agricultural Bureau of Shanxi, Xiangfen, Shanxi 041500, China)

Abstract:【Aim】*Porphyrophora sophorae* Arch. (Hemiptera: Coccomorpha: Margarodidae) is a species of soil-inhabiting scale insects. This study aims to relate the structure and adaptability of the antennae to the soil-inhabiting behaviors of *P. sophorae*.【Methods】The antennae and antennal sensilla of adult females of *P. sophorae* were observed under light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM).【Results】The results show that the antennae of adult females of *P. sophorae* are composed of nine segments. All of the antennal segments are short and wide, and the intersegments are compactly connected, which makes the antennae sturdy. A total of 29 – 48 sensilla in four types, *e. g.*, 2 – 5 Böhm's bristle (Bb), 5 – 12 aporous sensilla trichodea (ASt), 10 – 15 coeloconic sensilla (Co) and 11 – 22 multiporous pegs (Mp) are observed on the antennae. According to their structures, the sensilla Bb, ASt, Co and Mp are speculated to function as a proprioreceptor, tactile sensilla, thermo-/hygrosensory and olfactory sensilla, respectively. These sensilla are mainly located on three segments as follows: 2 – 4 Bb on the scape; 6 – 10 Co on the flagellomere F3; and the largest number of sensilla, including 3 – 8 Co, 4 – 11 ASt and 11 – 22 Mp on the flagellomere F7 (top segment). The other segments have almost no sensillum.【Conclusion】The antennae of the adult females of *P. sophorae* have many characteristics different from other scale insects, and these characteristics are adaptive to their soil-inhabiting behaviors.

Key words: *Porphyrophora sophorae*; soil-inhabiting; antennal morphology; sensillar distribution; ultrastructure

1 INTRODUCTION

The cochineal scales (genus *Porphyrophora*) are a group of soil-inhabiting scale insects in Margarodidae (Hemiptera: Coccomorpha). Currently, this genus contains 50 species. This group of scale insects is well known in the world, as some species have been used as sources of carmine dyes for several centuries in history. However, with the application of artificial dyes, these scale insects have lost their economic value and are currently considered as crop pests (Vahedi and Hodgson, 2007). Of these insects, *Porphyrophora sophorae* Arch. is an important pest of licorice (*Glycyrrhiza uralensis* Fisch), a traditional Chinese medicine material plant in Northwest China. Because *P. sophorae* spend most of its life underground, this insect damages the roots of licorice and causes a serious economic loss (Yang and Gao, 1998; Liu and Chen, 2008).

P. sophorae reproduces one generation per year in Northwest China. The newly hatched 1st instar nymphs of *P. sophorae* spend wintertime in underground oocysts and disperse in the second year from March to April (Yang and Gao, 1998; Liu and Chen, 2008). The 1st instar nymphs are the main performers of dispersion. They have a small and light body with developed antennae and legs, and thus, they can be passively spread for a long distance by wind and can actively wander to find host plants by crawling. In finding and locating host-plants, the antennae of the 1st instar nymphs play a very important role.

Once they dig into the ground and start feeding on the host plant root, the 1st instar nymphs molt into the 2nd instar nymphs. Unlike the 1st instar nymphs, the bodies of the 2nd instar nymphs are hardened, with a pearl-like cyst and have functional mouthparts for continuing to feed and grow, but their antennae and legs are vestigial. After the cyst stage, the adult females emerge. The adult females are neotenic, no longer feed, and have no wings and mouthparts, but have fully developed antennae and legs. The new

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作者简介：王旭，男，1983 年生，山西太原人，博士研究生，研究方向为蚧虫生理及其生物防治，E-mail：wx4546@163.com
* 通讯作者 Corresponding author, E-mail: xieyp@sxu.edu.cn
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emerged adult females bore out of the ground and wander over the surface of the ground to mate with males. After mating, the adult females dig into the ground and secrete wax threads to form an ovisac to lay eggs. Adult females usually do not lay eggs on the host-plant but 10 – 50 cm away from the host-plant (Liu *et al.*, 2016). The antennae of the adult females play an important role in the actions of locating the oviposition site.

The antennae are important peripheral sensory organs of insects and play an important role in seeking food, habitat, reproductive partners and the oviposition site. Antennal sensilla are basic function units of the antennae. According to the functions, these sensilla can be classified as chemoreceptors, mechanoreceptors, or thermoreceptors/hygroreceptors (Gullan and Cranston, 2005). Therefore, for the sensillar types, the quantity and distribution determine the functions of the antennae, and also can well reflect the evolutionary adaptation of the insects (Meng *et al.*, 2015). The antennal sensilla of the scale insects have been studied at the ultrastructure level only in a few of species, but the soil-inhabiting scale insects have not been involved (Le Rü *et al.*, 1995; Porcelli, 1995; Chiappini and Negri, 2004; Ahmad *et al.*, 2013; Wang *et al.*, 2016b).

Recently, we studied and reported the ultrastructure of the antennal sensilla of the 1st instar nymphs of *P. sophorae* (Wang *et al.*, 2016a) and found that the antennae of the adult females differ from those of the 1st instar nymphs in antennal morphology, segment, and sensilla type, quantity and distribution. These differences may be of significance for gaining a better understanding of the relationship of the antennal development, function and behaviors in nymphs and adult females.

In this study, we observed the antennae and antennal sensilla of adult females of *P. sophorae* under light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). The aim is to provide the ultrastructural data of the antennae and antennal sensilla and to discuss their possible functions and adaptabilities combined with the soil-inhabiting behaviors of the adult females. These data, plus the data from the 1st instar nymphs, should be of significance not only for understanding this species, *P. sophorae*, but also for understanding the soil-inhabiting scale insects.

2 MATERIAS AND METHODS

2.1 Insects

Adult females of *P. sophorae* emerge during late August to early September. In this period of 2014, newly emerged adult females were collected from a field of *G. uralensis* in Yanchi County of Ningxia Hui Autonomous Region of China.

2.2 Light microscopy observation

For the light-microscopy observation, the adult females of *P. sophorae* were first fixed with 75% ethanol and then soaked in an 8% NaOH solution at 40℃ overnight. By this treatment, the inner parts of the insect body were dissolved and only the cuticles with the antennae and legs remained. Then, the cuticles were stained with basic fuchsin and mounted on glass slides. Finally, the slide specimens were observed under a light microscope (Olympus BX-51, Olympus Co. Ltd., Japan). By observation, the distribution position and quantity of the antennal sensilla were recorded. At least 20 individuals were examined. In this study, the terminologies of Koteja (1980), Zacharuk (1980), Le Rü *et al.* (1995) and Wang *et al.* (2016a) were followed in naming the types of antennal sensilla.

2.3 Electron microscopy observation

For electron microscopy observation, the antennae of the adult females of *P. sophorae* were cut under a dissecting microscope and fixed in a solution of 2.5% (v/v) glutaraldehyde (phosphate-buffered saline 0.1 mol/L, pH 7.2) for 24 h at 4℃. Then, the preparation and observation of the antenna samples under SEM and TEM were conducted following the methodology used by Wang *et al.* (2016a).

3 RESULTS

3.1 Antennal morphology and sensillar distribution

The antennae of the adult females of *P. sophorae* (Fig. 1: A, B) are 480 – 650 μm in length and have a conical shape with a slightly inflated and hemispherical tip. In general, the antennae have nine segments, including the scape (SC, 48 – 95 μm long), pedicel (PE, 38 – 65 μm long), and flagellum of seven flagellomeres (F1 – F7, 46 – 65, 46 – 71, 58 – 87, 49 – 79, 44 – 68, 37 – 53, and 80 – 127 μm in length, respectively) (Fig. 1: A). However, in rare individuals, the antennae have eight segments, on which segments F6 and F7 are fused together (Fig. 1: B). The length and width of each segment are shown in the Table 1. The scape, pedicel and F1 – F6 have a similar short cylindrical shape, but the F7 have a hemispherical shape, and the width of these segments is obviously larger than the length. The scape is membranous or lightly sclerotized, while the other segments are strongly sclerotized. These segments connect to each other compactly at the intersegments (Fig. 1: A).

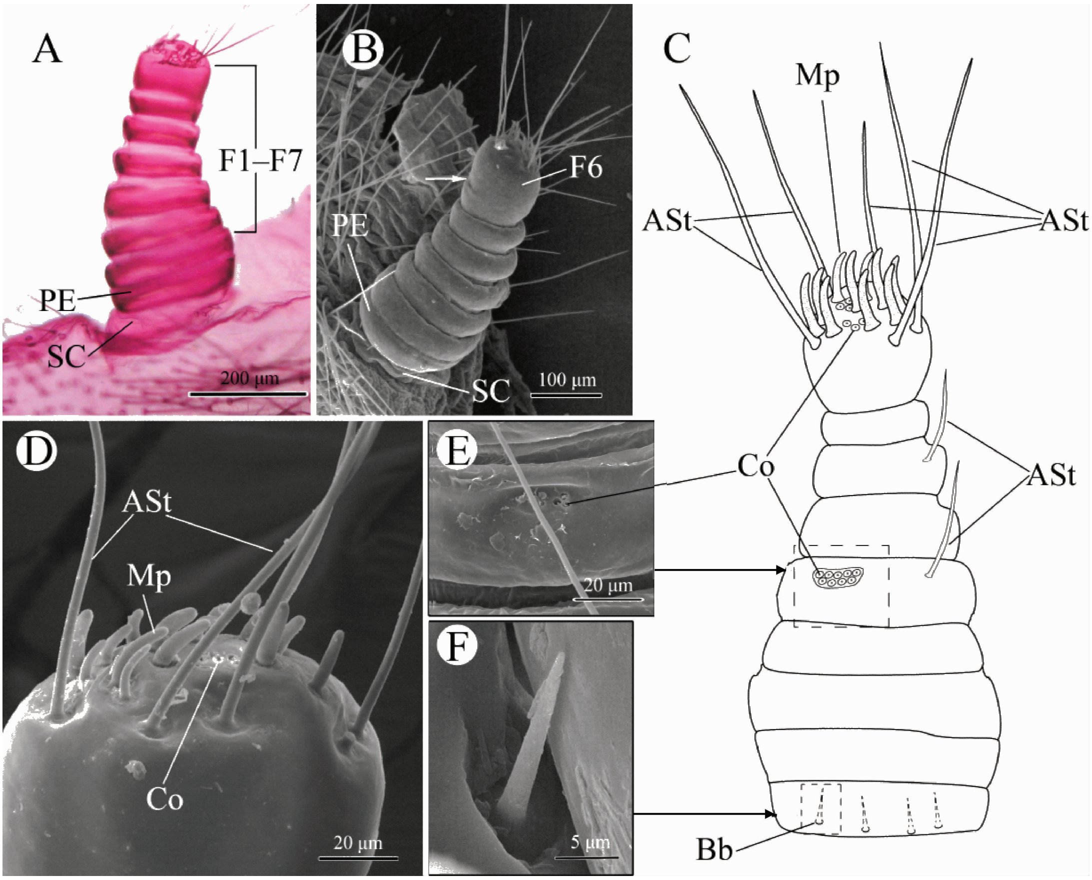

Fig. 1 Antennae of adult females of *Porphyrophora sophorae*

A: Light microscopy (LM) photograph of a nine-segmented antenna, showing the membranous scape (SC), the sclerotized pedicel (PE) and seven flagellomeres (F1 – F7). B: Scanning electron microscopy (SEM) photograph of an eight-segmented antenna, showing an uncomplete constriction (arrow) on the top segment, as if it is formed by the F6 and F7 combination. C: Schematic representation of the distribution of the sensilla on the antennae (nine-segmented, ventral view). The sensilla on the ventral side of the antennae are indicated by the solid line and the sensilla on the dorsal side are shown by the dotted lines. D: SEM photograph of the segment F7, showing the sensilla in the cluster on the top of the segment, in which, the sensilla ASt are on the peripheral side, while Mp and Co are in the middle. E: SEM photograph of the segment F3, showing the cuticle depression on the segment and the sensilla Co in a cluster in the depression. F: SEM photograph of the base of the scape, showing one sensillum Bb.

In total, 29 – 48 sensilla (mean ± *SD* = 38.10 ± 4.51) are observed on each antenna. Based on the ultrastructure, these sensilla are classified into four types as follows: (i) 2 – 5 Böhm's bristles (Bb) (mean ± *SD* = 2.80 ± 0.89); (ii) 5 – 12 aporous sensilla trichodea (ASt) (mean ± *SD* = 8.25 ± 2.00); (iii) 10 – 15 coeloconic sensilla (Co) (mean ± *SD* = 12.45 ± 1.96); and (iv) 11 – 22 multiporous pegs (Mp) (mean ± *SD* = 14.60 ± 2.95). The appearance, distribution and structure characteristics of these sensilla are shown in Fig. 1 (C) and Table 2.

These sensilla are mainly distributed on three antennal segments, the scape, F3, and F7. On the scape, 2 – 4 Bb are present on the dorsal side at the proximal end. On segment F3, there is a shallow cuticle depression at the ventral side where 6 – 10 Co cluster (Fig. 1: C, E). Occasionally, 1 – 2 ASt or one Mp is also present on F3. The segment F7 (the top antennal segment) possesses the most types and quantities of sensilla on the antennae, including 4 – 11 ASt, 3 – 8 Co and 11 – 22 Mp. These sensilla are all distributed on the top, where the ASt are peripherally located, and the Co and Mp are in the middle position (Fig. 1: D). The other antennal segments usually have no sensillum. In individual cases, the pedicel has one Bb on the ventral side, and the segments F1, F2, F4 and F5 might have one ASt (Table 2).

3.2 Antennal sensilla

3.2.1 Böhm's bristles (Bb): The sensilla Bb are 2 – 4 short setaes located on the dorsal side at the proximal end of the scape. Individually, one Bb is also present on the ventral side of the pedicel. The shaft of Bb is straight with a tapering top, 13 – 27 μm in length and 2.1 – 3.5 μm wide at the base of the shaft and is inserted into a flexible socket (Table 2; Fig. 1: F).

3.2.2 Aporous sensilla trichodea (ASt): The majority of the sensilla ASt are located on the top

antennal segment (F7), and the minority of ASt are present on the segments F1 – F5 (Table 2). The shafts of the sensilla ASt are long, curved, and hair-like, with 150 – 270 μm in length and 3.6 – 4.7 μm in width at the base that inserted into a flexible socket (Table 2; Fig. 2: A). In general, the ASt on the top antennal segment are obviously longer than those on other segments. The cuticular wall (cW) of the shaft is over 0.8 μm in thickness, single layered, and aporous. The shaft lumen is filled with electronic density materials but no dendrite (Fig. 2: B). The ASt is innervated by a single neuron that terminates with a tubular body (tB) below the socket (Fig. 2: C). At the tubular body level, the socket of the ASt is very large (over 10 μm in width), and the cuticular wall of the socket has multiple rings that show an annual growth ring pattern. At a more proximal level, the outer dendritic segment (oD) is observed in the sensillum lymph cavity (Fig. 2: D).

Table 1 The size of the antennae of adult females of *Porphyrophora sophorae* (*n* = 20)

Segments	Length (μm)		Width (μm)	
	Range	Mean ± *SD*	Range	Mean ± *SD*
SC	48 – 95	65.3 ± 13.2	220 – 277	246.3 ± 20.4
PE	38 – 65	53.7 ± 7.3	204 – 279	241.3 ± 19.6
F1	46 – 65	53.7 ± 5.8	204 – 279	245.3 ± 21.1
F2	46 – 71	57.3 ± 6.2	177 – 253	223.0 ± 22.4
F3	58 – 87	67.5 ± 6.4	162 – 227	195.9 ± 19.3
F4	49 – 79	61.0 ± 6.8	139 – 198	163.1 ± 16.0
F5	44 – 68	54.0 ± 7.0	116 – 166	138.5 ± 13.8
F6	37 – 53	44.6 ± 4.3	100 – 149	125.5 ± 13.4
F7	80 – 127	99.3 ± 11.6	107 – 150	128.5 ± 11.4
Total	484 – 646	556.4 ± 42.1	–	–

Table 2 Distribution and characteristics of the antennal sensilla in adult females of *Porphyrophora sophorae* (*n* = 20)

Sensilla	Distribution (number, mean ± *SD*)	Porous aspect	Surface	Socket	Length (μm)	Width (μm)	Putative function
Bb	SC (2 – 4, 2.65 ± 0.67), PE (0 – 1, 0.15 ± 0.37)	Aporous	Smooth	Flexible	19.61 ± 4.42	2.67 ± 0.36	Mechanosensory
ASt	F1 (0 – 1, 0.10 ± 0.31), F2 (0 – 1, 0.05 ± 0.22), F3 (0 – 2, 0.55 ± 0.76), F4 (0 – 1, 0.10 ± 0.31), F5 (0 – 1, 0.15 ± 0.37), F7 (4 – 11, 7.35 ± 1.81)	Aporous	Smooth	Flexible	213.55 ± 38.55	4.15 ± 0.32	Mechanosensory
Co	F3 (6 – 10, 7.35 ± 1.31), F7 (3 – 8, 5.05 ± 1.23)	Aporous	Smooth	Inflexible	6.45 ± 0.36	1.78 ± 0.28	Thermo-/hygrosensory
Mp	F3 (0 – 1, 0.20 ± 0.41), F7 (11 – 22, 14.4 ± 2.82)	Multiporous	Pitted	Inflexible	21.18 ± 4.65	4.38 ± 1.02	Olfactory

Data of sensillar length and width in the table are mean ± *SD*.

3.2.3 Coeloconic sensilla (Co): The sensilla Co are aporous small setae that are 6 – 7 μm long and 1.4 – 2.3 μm wide at the base (Table 2). Each seta grows in a deep crater (approximately 6 – 7 μm in deep) on the antennae (Fig. 3: A). The base of the seta is inserted into an inflexible socket (Fig. 3: D). The sensilla Co are located on the segment F3 and the top antennal segment (F6 or F7). Of which, 6 – 10 Co occur in a cluster in the cuticle depression on the segment F3 as shown in Fig. 1 (C). The other 3 – 8 Co are located on the tip of the top segment and usually are 2 – 3 in a group (Fig. 1: C; Fig. 3: A). Cross-sections of three Co at the shaft level (Fig. 3: B) show that the three shafts are located at the center of the crater cavity (Cv). The invaginated cuticle (Cu) and the sensillum lymph cavity (SL) of the Co are visible. Each Co is innervated by three neurons, of which, two of their outer dendritic segments (oD) extend into the shaft lumen (Fig. 3: C) and the other one terminates at the base of the shaft (Fig. 3: D).

3.2.4 Multiporous pegs (Mp): The sensilla Mp are mainly distributed on the top antennal segment (F7). Occasionally, one Mp is present on the segment F3. The Mp can be described as "curved fleshy seta". The shafts are finger-like and inserted into an inflexible socket (Fig. 4: A). The shafts of the Mp vary greatly in size with 9 – 28 μm in length

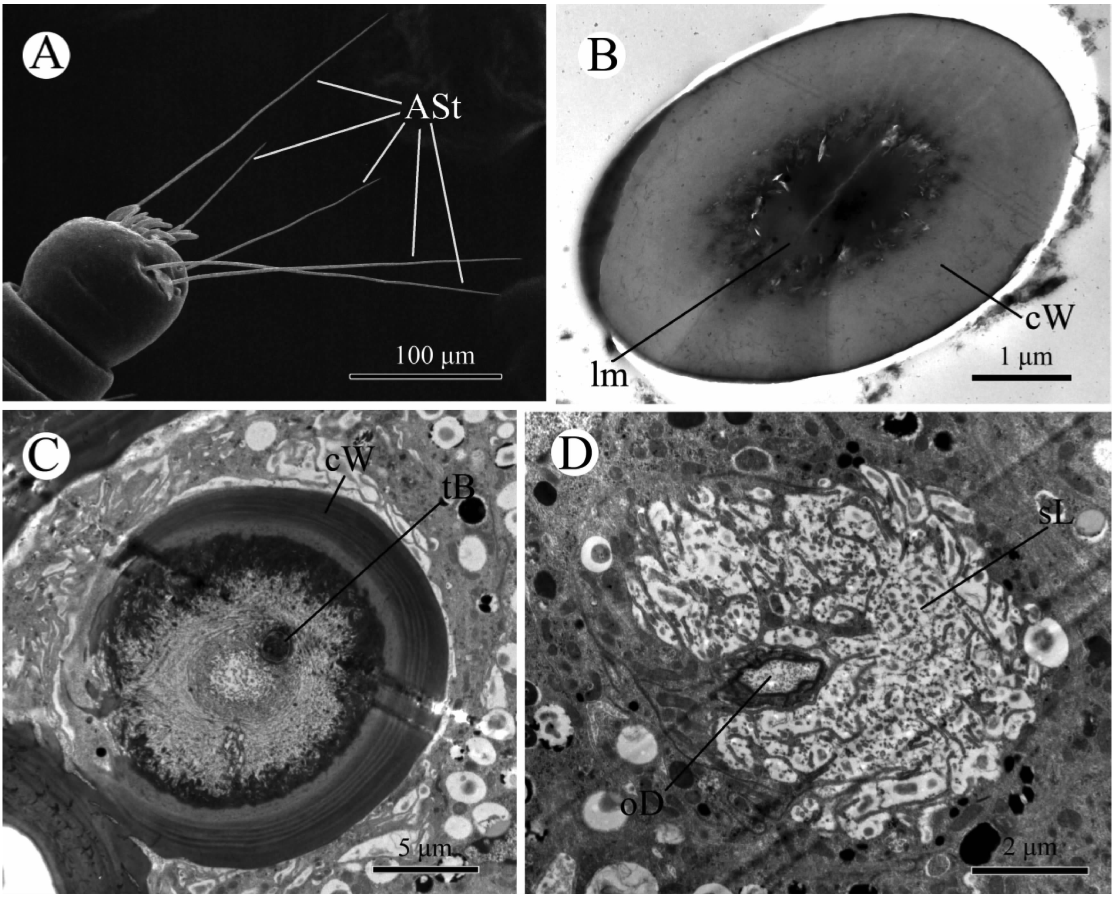

Fig. 2 Observation of the aporous sensilla trichodea (ASt) under scanning electron microscopy (SEM) (A) and transmission electron microscopy (TEM) (B – D)

A: The top antennal segment (F7), showing five ASt on top of the segment. B: The cross-section of the shaft, showing the cuticular wall (cW) with a single layer that is aporous, and the shaft lumen (lm) with electronic density materials. C: Cross-section at the socket level, showing the tubular body (tB) and the cuticular wall (cW) of the socket with a multiple ring pattern. D: Cross-section at a level of more proximal than in Fig. C, showing one outer dendritic segment (oD) in the sensillum lymph cavity (sL).

and 2.3 – 5.6 μm in width at the base as shown in Fig. 1(D). The surface of the shaft is not smooth but pitted (Fig. 4: A). The cross sections of the shaft of Mp (Fig. 4: B) show numerous pores (p) on the shaft. It is these pores that cause the surface of the shaft to be pitted. These pores lead to the shaft lumen through the culticular wall of the shaft. Pore tubules (pT) are obvious in the pores, and over 17 dendritic branches (dB) are observed in the shaft lumen (Fig. 4: B)

4 DISCUSSION AND CONCLUSION

P. sophorae is a typical soil-inhabiting scale insect. The antennae are present on the 1st instar nymphs, adult females and adult males, but vestigial in the 2nd instar nymphs. The antennae of the 1st instar nymphs are important for the scale insect dispersing (Liu *et al.*, 2016), while the absence of the antennae is associated with the behavior of the 2nd instar nymphs feeding sedentarily on the roots of the host plants. After the 2nd nymphal instar, the female scale insects develop into adult stage and have a pair of developed antennae again. In the adult stage, the antennae play an important role in adult females boring out under-ground, mating with adult males, and searching for oviposition sites in the ground. Therefore, the antennae of *P. sophorae*, as important peripheral sensory organs, fully adapt to the soil-inhabiting behavior of the scale insect. It is interesting that, in the current study, the antennae of the adult females of *P. sophorae* provide several novel characteristics compared with the antennae of the 1st instar nymphs (Wang *et al.*, 2016a) and the adult females of other species of scale insects, which have previously been studied at the ultrastructure level (Le Rü *et al.*, 1995; Wang *et al.*, 2016b).

4.1 Antennal morphology

The antennae of the adult females of *P. sophorae* have nine segments (Fig. 1: A) or rarely, have eight segments. In the latter case, segments F6 and F7 are fused together (Fig. 1: B). Although the antennal segments with nine is similar to the antennae

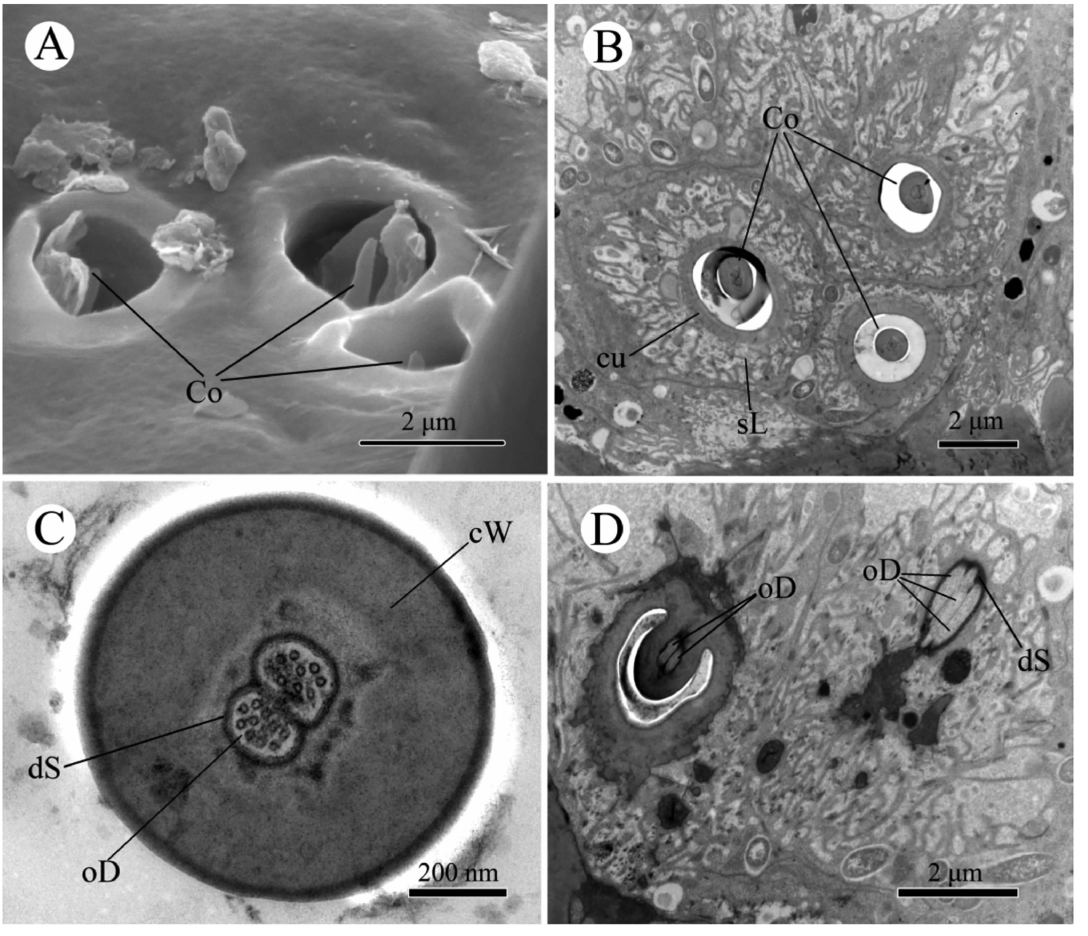

Fig. 3　Observation of the coeloconic sensilla (Co) under scanning electron microscopy (SEM) (A) and transmission electron microscopy (TEM) (B–D)

A: Three Co observed on the top antennal segment. B: Cross-section at the level of the shaft, showing the shafts of the three Co, the invaginated cuticle (cu) and the sensillum lymph cavity (sL). C: The magnified view of one Co shaft, showing the shaft with the aporous and single layer cuticular wall (cW), and the two outer dendritic segments (oD) that are enveloped by dendritic sheaths (dS) in the shaft lumen. D: Cross-section of two Co. The left one is at the socket level, showing the inflexible socket and the two outer dendritic segments (oD) in the shaft lumen, while the right one is at a more proximal level, showing three oD that are enveloped by dendritic sheaths (dS).

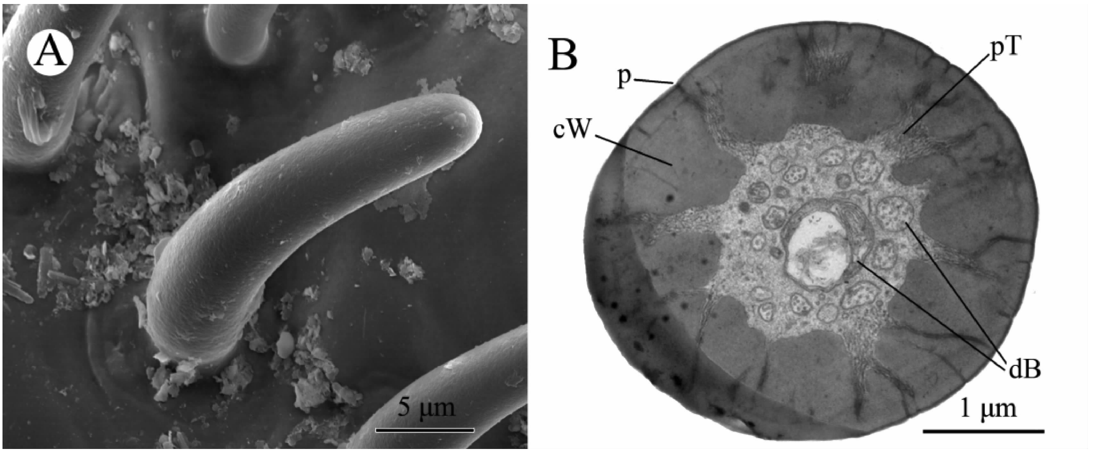

Fig. 4　Observation of the multiporous peg sensilla under scanning electron microscopy (SEM) (A) and transmission electron microscopy (TEM) (B)

A: Photograph of one Mp, showing its finger-like shaft with a pitted surface. B: Cross-section at the shaft, showing many pores (p) through the cuticular wall (cW) of the shaft, the pore tubules (pT) in pores, and more than 17 dendritic branches (dB) in the shaft lumen.

of the adult females of *Phenacoccus manihoti* (Matile-Ferrero) (Pseudococcidae) (Le Rü *et al.*, 1995) and *Matsucoccus matsumurae* (Kuwana) (Matsucoccidae) (Wang *et al.*, 2016b), the antennae of the adult females of *P. sophorae* have two obvious features in morphology. First, the antennae of the adult females of *P. sophorae* are sturdier. Their length is approximately 556.4 ± 42.1 μm, and their width is 246.3 ± 20.4 μm. The ratio of the length to width is approximately 2.3:1 (Table 1). In comparison, the antennae of the adult females of *P. manihoti* and *M. matsumurae* are approximately 650 – 850 μm in length and 100 – 150 μm in width. The ratio of the length to width is over 4.3:1. Second, except for the top segment, the other antennae segments of the adult females of *P. sophorae* all have cylindrical shapes, with much larger widths than lengths (Table 1). The adjacent segments are connected compactly, and the constriction at each intersegment of the antennae is not obvious. However, the antennal segments of *P. manihoti* and *M. matsumurae* are relatively slender, and obviously narrowed at the intersegment. These features make the antennae of the adult females of *P. sophorae* have less flexibility and a higher strength. This allows them to adapt to their soil-inhabiting behavior to avoid the antennae being broken while the females are exploring in the soil. In addition, the scape of the adult females of *P. sophorae* is membranous or lightly sclerotized. This segment might be responsible for adjusting the angle of the antenna.

4.2 Antennal sensilla

In the adult females of *P. sophorae*, a total of four types of sensilla on the antennae are observed, and these sensilla have different distributions, morphologies and structures and perform different functions.

4.2.1 Böhm's bristles (Bb): The first type is the sensilla Bb. It is a type of mechanoreceptor and is commonly distributed on the scape and pedicel of the insect antennae. The sensilla Bb are considered to have the function of proprioreceptors and play a role in monitoring the positions of the antennae (Schneider, 1964; Mclver, 1975). For the adult females of *P. sophorae*, 2 – 4 Bb are located on the dorsal side at the proximal end of the scape, and another one is occasionally present on the ventral side of the pedicel. Their function might be to sense and respond to the adjustment of the relative location of the antennae to the head.

In comparison, as the same species, the antennae of the 1st instar nymphs of *P. sophorae* have only one Bb on the scape (Wang *et al.*, 2016a). While in a species of the family Matsucoccidae, the antennae of *M. matsumurae* in the adult female stage have 9 – 16 Bb on the scape (Wang *et al.*, 2016b). Contrarily, the antennae of the adult females of *P. manihoti*, a species of Pseudococcidae, have no sensillum Bb on the scape and pedicel, but have four trichoid sensilla (Le Rü *et al.*, 1995). These trichoid sensilla may perform the function of Bb.

4.2.2 Aporous sensilla trichodea (ASt): The second type of sensilla is the ASt. The sensilla ASt are characterized by very long and aporous shafts and a single neuron that terminates with a tubular body below the socket. These characteristics show that ASt are mechanoreceptors (Mclver, 1975; Keil, 2012). Their functions are to detect the stimuli of tactile from the surrounding environment (Mclver, 1975; Gullan and Cranston, 2005). In adult females of *P. sophorae*, these ASt have a very strong shaft: their shafts are long (150 – 270 μm), thick (3.6 – 4.7 μm at the base) and have a thick cuticular walls (0.8 μm), and their sockets are wider (over 10 μm). These ASt are distributed with the sensilla Co and Mp on the antennal tip, and they are located peripherally and around the sensilla Co and Mp (Fig. 1: C, D). These characteristics in morphology and distribution, as indicated in the sensilla ASt, may play not only a sensory function but also a protective function for the sensilla Co and Mp on the antennal tip.

4.2.3 Coeloconic sensilla (Co): The third type of sensilla is Co. The shaft of Co is aporous and inserted into an inflexible socket. Each Co is innervated by three neurons. In the three dendrites, two extend into the shaft lumen, while another one terminates at the shaft base. These features are typical of thermo-/hygrosensory sensilla (Altner and Prillinger, 1980; Altner *et al.*, 1983; Haug, 1985; Steinbrecht, 1998). The similar sensilla are also present on the antennae of the 1st instar nymphs of *P. sophorae* and were considered to function as thermo-/hygrosensory sensilla (Wang *et al.*, 2016a). In fact, the sensilla Co are common on the antennae of scale insects, *e.g.*, on the antennae of adult females of *P. manihoti* and *M. matsumurae* (Le Rü *et al.*, 1995; Wang *et al.*, 2016b) and adult males of *Quadraspidiotus perniciosus* Comstock (Diaspididae) and *M. matsumurae* (Chiappini and Negri, 2004; Wang *et al.*, 2016b). They were all considered as thermo-/hygrosensory sensilla. Thus, the sensilla Co on the adult females of *P. sophorae* might have the same functions as the thermo-/hygrosensory sensilla. However, the distribution

style of the Co in the adult females of *P. sophorae* is unique: the sensilla Co are clustered on the segment F3 and the top antennal segment. This distribution style is different not only to the 1st instar nymphs of *P. sophorae* but also to the prior studied species of scale insects. The 1st instar nymphs of *P. sophorae* have only two Co, and they are located only on the top segment (Wang *et al.* 2016a). The adult females of *P. manihoti* have three Co, of which, one is located on the segment F1 and the other two are on the top segment (Le Rü *et al.*, 1995). The adult females of *M. matsumurae* have 3 – 10 Co, and each flagellomere has 0 – 3 Co, except for the top segment (Wang *et al.*, 2016b). The adult females of *P. sophorae* possess so many Co that it may mean that the temperature and humidity are very important factors for the adult females of *P. sophorae* to locate the oviposition sites. It is easy to understand that the temperature and humidity of the oviposition sites should greatly influence the survival and hatching of the eggs of *P. sophorae*.

4.2.4 Multiporous pegs (Mp): The 4th type of sensilla is the Mp. The Mp possess typical characteristics of olfactory sensilla. The shaft is single-walled and multiporous, and the dendrites have numerous branches in the shaft lumen (Zacharuk, 1980; Altner and Prillinger, 1980; Steinbrecht, 1999). Thus, it was believed that the Mp of *P. sophorae* are olfactory sensilla that perform the function in the adult females to detect the volatile compounds released from the host plants. That is significant since in such way the adult females can lay eggs far enough from the host plants. However, the antennae of the 1st instar nymphs of *P. sophorae* have two subtypes of olfactory sensilla, the straight multiporous peg and the curvy multiporous peg (Wang *et al.*, 2016a). In morphology and structure, the curvy multiporous peg is similar to the olfactory sensilla Mp of the adult females. Another characteristic is that far more olfactory sensilla Mp (11 – 22) are present in the adult females of *P. sophorae* and totally concentrated on the antennal top. It may mean that the plant volatiles are the most important cues for *P. sophorae* to locate the host plants. In comparison, only eight olfactory sensilla are present on the antennae of the adult females of *P. manihoti* and *M. matsumurae*, and they are separated on the last three segments (*P. manihoti*) or four segments (*M. matsumurae*) (Le Rü *et al.*, 1995; Wang *et al.*, 2016b).

4.2.5 The absent sensilla on the antennae: In comparison, there are fewer types of sensilla on the antennae of the adult females of *P. sophorae*, and several types of sensilla are absent. For example, the Johnston's organ (Jo) and the campaniform sensillum (Ca) are present on the pedicel of the 1st instar nymphs of *P. sophorae* (Wang *et al.*, 2016a). The sensillum Jo has no obvious structure outside the cuticle, and thus, that it is difficult to be observed. The sensilla Ca are very common on the antennae of scale insects (Koteja, 1980) and observed on the pedicel in the antennae of both the 1st instar nymphs and adult females of *P. manihoti* and *M. matsumurae* (Le Rü *et al.*, 1995; Wang *et al.*, 2016a, 2016b). The sensillum Ca on the pedicel usually performs the function of monitoring the swing movement of the flagellum (Schneider, 1964; Mclver, 1975; Porcelli, 1995; Wang *et al.*, 2016b). Unlike in other species, in the adult females of *P. sophorae*, the pedicel and F1 are similar in size and shape and connected compactly (Fig. 1: A, B). These may limit the swing movement of the flagellum and explain why the sensillum Ca might not be necessary.

Another type of sensilla that is absent is the gustatory sensilla on the antennae of the adult females of *P. sophorae*. Insect antennae usually have chemoreceptors, including olfactory sensilla and gustatory sensilla. In prior studies, some gustatory sensilla have been observed on the top antennal segment of scale insects, *e.g.*, *P. manihoti* (Le Rü *et al.*, 1995), *Kerria lacca* (Kerr) (Tachardiidae) (Ahmad *et al.*, 2013), and *M. matsumurae* (Wang *et al.*, 2016b). However, the gustatory sensilla were not observed on the antennae of both the adult females and 1st instar nymphs of *P. sophorae* (Wang *et al.*, 2016a). In general, the rhizophagous insects usually have gustatory sensilla to detect the water-soluble substances released by the host-plant roots (Eilers *et al.*, 2012). The reason for the absence of gustatory sensilla on the antennae of *P. sophorae* is not clear.

4.2.6 The sensillar distribution style on the antennae: On the antennae of *P. sophorae*, the sensilla are mainly distributed on three segments, the scape, F3 and F7 (the top segment), and almost not present on other antennal segments. The scape of the adult females of *P. sophorae* with only 2 – 4 Bb should be responsible for adjusting the antennae relative to the location of the head. The segment F3 has 6 – 10 Co and occasionally one Mp or 1 – 2 ASt. This segment should be mainly responsible for detecting the temperature and humidity in the environment. The top antennal segment has the largest number of sensilla, including 3 – 8 Co, 4 – 11 ASt and 11 – 22 Mp. It should be

the most important functional area on the antennae, where the multiple functions of touch sense, olfactory reception, and the temperature and humidity sense are assembled.

Such a sensillar distribution style is very different from that of the adult females of *P. manihoti* and *M. matsumurae* (Le Rü *et al*., 1995; Wang *et al*., 2016b). That should be advantageous for the adult females to explore in the soil. However, the antennae of adult females of *P. sophorae* are also different from those of 1st instar nymphs (Wang *et al*., 2016a). From a developmental view, the antennae are vestigial in the 2nd instar nymphs, which might be one of the reasons of these differences. Meanwhile, the different characteristics of the antennae might be to meet the different behaviors displayed by 1st instar nymphs and adult females of *P. sophorae*.

4.3 Conclusion

As mentioned above, adult females of *P. sophorae* have a pair of stubby antennae on which there are four types of sensilla, including 2 – 5 Bb (proprioreceptor), 5 – 12 ASt (tactile sensilla), 10 – 15 Co (thermo-/hygrosensory sensilla) and 11 – 22 Mp (olfactory sensilla). These sensilla are mainly located on the segments scape, F3 and F7 (top segment). The top segment has the vast majority of sensilla and is the most important functional area on the antennae. The morphology and sensillar distribution of the antennae are greatly adapted to their special soil-inhabiting behaviors.

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甘草胭脂蚧雌成虫触角感受器超微结构

王 旭[1]，谢映平[1,*]，张艳峰[1]，刘卫敏[1]，王全亮[2]

（1. 山西大学生命科学学院，太原 030006；2. 山西省襄汾县农业局，山西襄汾 041500）

摘要：【目的】甘草胭脂蚧 *Porphyrophora sophorae* Arch. 是一种典型的土栖性蚧虫。本研究旨在了解该虫触角的结构及其对土栖环境的适应性。【方法】利用光学显微镜、扫描和透射电子显微镜对甘草胭脂蚧雌成虫触角以及触角感受器进行了观察。【结果】甘草胭脂蚧雌成虫触角由 9 节组成，各触角节粗而短，各节间连接紧密，使触角形态呈现出较为粗壮的特点。在触角上分布着 4 种感受器 29 ~ 48 个，包括 2 ~ 5 个 Böhm 氏鬃毛，5 ~ 12 个无孔毛形感受器，10 ~ 15 个腔锥形感受器和 11 ~ 22 个多孔钉形感受器。根据各感受器的结构特点，判断它们分别具有自体感受、触觉感受、温湿度感受和嗅觉感受的功能。触角感受器主要分布在触角的 3 个节上，分别是：柄节，具 2 ~ 4 个 Böhm 氏鬃毛；第 3 鞭节，分布有 6 ~ 10 个腔锥形感受器；第 7 鞭节（即顶节），大多数的感受器都分布在这一节的端部，包括 3 ~ 8 个腔锥形感受器，4 ~ 11 个无孔毛形感受器和 11 ~ 22 个多孔钉形感受器。而在触角的其他节上几乎没有感受器分布。【结论】甘草胭脂蚧雌成虫触角有着许多不同于其他蚧虫触角的特点，这些特点是与其土栖性的生活方式相适应的。

关键词： 甘草胭脂蚧；土栖；触角形态；感受器分布；超微结构

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